

# Species distribution model and population dynamics of invasive alien plant *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java, Indonesia

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**Abstract.** Nasihin I, Widhiono I, Sudiana E, Nurdin, Herlina N, Imaningsih W. 2024. Species distribution model and population dynamics of invasive alien plant *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java, Indonesia. *Biodiversitas* 25: 4806-4815. Invasive alien plants are a serious threat to conservation areas since they will threaten biodiversity by over-dominating species composition and reducing diversity. However, conservation area managers have not taken invasive alien plant management seriously. *Calliandra calothyrsus* is one of the invasive alien plant species that has been reported to occur in conservation areas. The purpose of this study was to develop a habitat suitability model and investigate population dynamics of *C. calothyrsus* in Gunung Ciremai National Park (GCNP), West Java Province, Indonesia. Maximum Entropy (MaxEnt) was used to build the model using 13 environmental predictors, including climate, physical, and soil characteristic variables. Population structure data were collected from 98 sampling plots, each measuring 10x10 m. The population dynamics and distribution of *C. calothyrsus* populations were analyzed using RangeShifter software with 50 years of simulation. The results showed an AUC value of >0.80, indicating the distribution model of *C. calothyrsus* has a high level of agreement between the model prediction and actual observation. Simulation analysis shows that the population of *C. calothyrsus* in GCNP will continue to increase over the next 50 years and spread throughout the park from where the occurrences of *C. calothyrsus* were recorded. The findings of this study suggest that managing the growth of the *C. calothyrsus* population from seedling to sapling is necessary, while restoring bare ground and shrub can prevent the spread of *C. calothyrsus*.

**Keywords:** *Calliandra calothyrsus*, conservation areas, invasive alien plant, population dynamic, species distribution

## INTRODUCTION

Conservation areas are key to local and global efforts to protect biodiversity and its ecosystems as well as to mitigate climate change and halt environmental degradation (Li et al. 2021; McCarthy et al. 2021; Yang et al. 2021; Marques et al. 2022; Sæþórðóttir et al. 2022). Nevertheless, various anthropogenic activities affect conservation areas, resulting in the loss of natural vegetation, fires, and invasion of alien species (Marques et al. 2022). Invasive alien species are organisms that thrive in certain ecosystems and cause economic and environmental losses to humans, animals and plants (Reaser et al. 2020). Invasive alien plants generally have widespread distribution with rapid expansion since they produce a large number of offspring (Ratnayake 2014). While the first introduction of invasive alien species is generally brought by human movement, their increasing spread is largely caused by deforestation, habitat degradation and climate change (Dermawan et al. 2018; Guo et al. 2018; Shrestha et al. 2018; Saranya et al. 2021).

Invasive alien species are problematic since they now also occur in several conservation areas, including in Gunung Ciremai National Park (GCNP), West Java

Province, Indonesia (Dewi et al. 2022; Supartono et al. 2023). This is a major threat to conservation areas, both in terms of biodiversity and legal certainty of the park (Foxcroft et al. 2017; Csiszár et al. 2020). In conservation areas, the rapid expansion of invasive alien species overdominates native biodiversity, changing the floristic and faunistic composition of the ecosystem (Kariyawasam et al. 2020). Furthermore, invasive alien species will reduce the effective area, change the boundaries and loss of legitimacy, resulting in Protected Areas Downgrading, Downsizing, and Degazettement (PADDD), which refers to the legal process of reducing the size or status of a protected area (Moodley et al. 2020).

The impacts of invasive alien species have explicitly been reported in several studies. For example, *Lantana camara* can change the physical, chemical, and biological properties of soil (Osunkoya and Perrett 2010; Rai 2012, 2015; Kannan et al. 2014, et al. 2016; Wang et al. 2015a,b; Panda et al. 2017; Shrestha et al. 2018; Kumar et al. 2021). *Mikania micrantha* has harmful impacts on the environment and economy, especially under climate change conditions (Guo et al. 2018). *Acacia nilotica* (L.) Willd. ex Delile causes a decrease in the quality of pasture (Dermawan et al. 2018), while *Chromolaena odorata* (L.)

R.M.King & H.Rob. causes loss of native vegetation (Shrestha et al. 2018; Saranya et al. 2021). *Calliandra calothyrsus* Meisn. is one of invasive alien plant species recorded in conservation areas in Indonesia (Setyawati et al. 2015; Tjitrosoedirjo et al. 2016). In GCNP, *C. calothyrsus* has occupied an area of 302.62 ha and spread at an altitude of 600-1500 masl, including in the utilization zone, rehabilitation zone, and jungle zone (BTNGC 2015; Supartono et al. 2023). *C. Calothyrsus* was introduced to the Mount Ciremai forest area in 1973 as an intercrop and firewood plant when the forest was still functioning as a production forest under the management of Perum Perhutani (BTNGC 2015).

The role and function of GCNP in biodiversity conservation are very important. Management of invasive species in this area, including prevention of introduction, colonization and spread, eradication, and control of existing populations, needs to be done to minimize the risk of invasiveness. Invasive species need time to adapt to new habitats which are influenced by the characteristics of the growth phase, taxonomy and environmental factors that will affect the level of invasiveness (Wang et al. 2018). Biodiversity management in conservation areas requires spatial information as one of the management strategies (Yudaputra 2020). Spatial information related to invasive alien species that pose a threat to conservation areas might serve to develop mitigation strategy to save the biodiversity (Kariyawasam et al. 2020; Moodley et al. 2020; Yudaputra 2020; Falcón-Brindis et al. 2021; Marques et al. 2022).

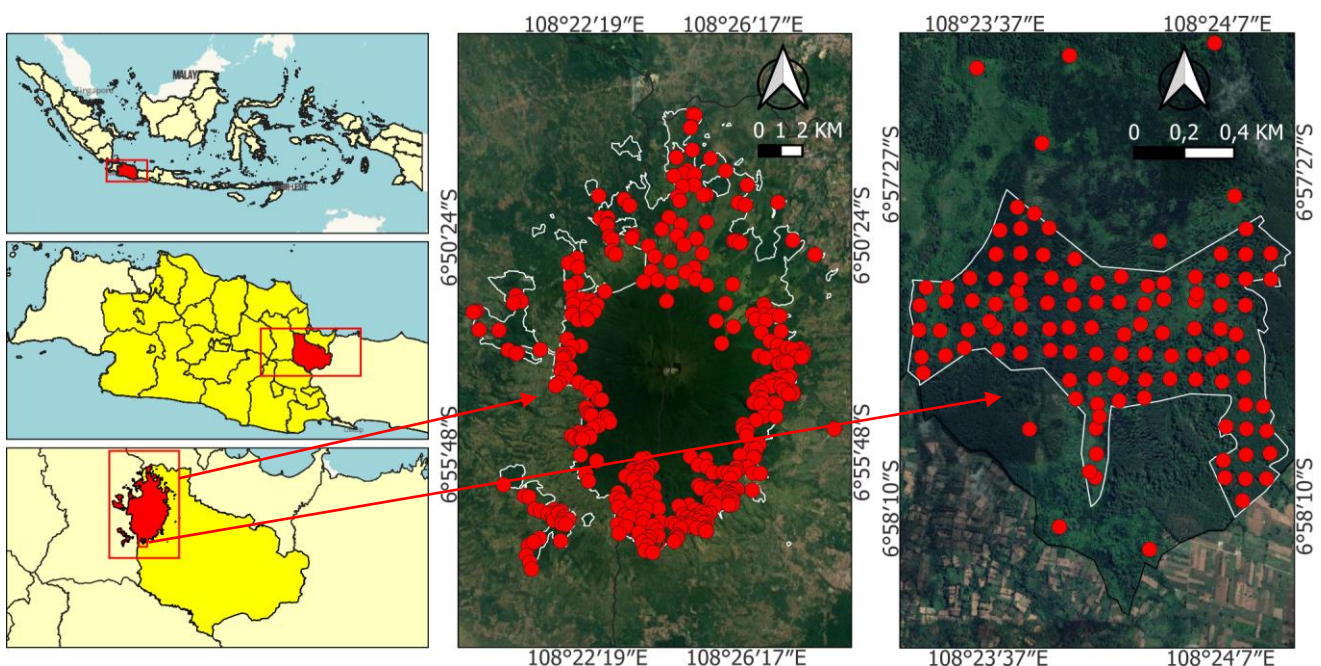
Prevention is a more effective strategy than controlling or eradication of alien species (Braun et al. 2016). Early detection, followed by rapid control and eradication of invasive species while they are still in establishment stage, is an effective way to reduce their spread. The use of

ecological niche models is essential to identify ecologically suitable areas to monitor and respond rapidly invasive species (Merow et al. 2014; Srivastava et al. 2019; Yan et al. 2020). The study on the distribution model and population dynamics of *C. calothyrsus* at an island scale has been carried out in Bali Island (Yudaputra 2020). Thus, it is essential to understand the distribution model and population dynamics of *C. calothyrsus* at a smaller and local scale as part of efforts to manage invasive alien plants. The purpose of this study was to develop a species distribution model and population dynamics of *C. calothyrsus* in GCNP and to understand the factors that influence its presence in the park. We expected the results of this study might serve as considerations in managing invasive alien plants, especially *C. calothyrsus*, in GCNP and other conservation areas.

## MATERIALS AND METHODS

### Study area

The research was conducted in the GCNP area at geographical position of 108°19'18" - 108°29'30" E and 6°46'57" - 6°58'57" S, covering an extent of 14,841.30 Ha (Figure 1). Land cover types in the park consisted of natural forests (32.97%), pine plantations (33.47%), shrubs (18.47%), and bareland (15.09%). Slope classes consisted of flat (3.76%), gentle (8.87%), rather steep (18.83%), steep (38.72%), and very steep (29.82%). Soil types are andic dystrodepts (31.25%), humic dystrodepts (1.87%), oxyaquic eutrudepts (0.22%), typic dystrodepts (5.23%), typic eutrudepts (23.73%), typic hapludands (37.47%), and typic udorthents (0.22%).



**Figure 1.** Map of research location in Karang Sari, Gunung Ciremai National Park, Kuningan, West Java Province, Indonesia, showing the occurrence records of *Calliandra calothyrsus* and population data collection at Karang Sari Research Station (left bottom)

Rainfall ranges from 2500-3000 mm/year, and the average temperature ranges from 17-25°C. The collection of population data of *C. calothyrsus* was conducted at the Karangsari Research Station, GCNP. Meanwhile, data collection on the occurrences of *C. calothyrsus* was conducted throughout the GCNP area.

### Data collection procedures

The data needed to build the distribution model of *C. calothyrsus* are species occurrence data and environmental variables. Species occurrence data are essential in developing the model structure which include species presence-absence and abundance. In this study, the data used was species presence data. The presence data of *C. calothyrsus* was collected through field surveys and data from the 2015 GCNP Invasive Plant Mapping and Control Report (BTNGC 2015).

Environmental variables are commonly used in species distribution modeling, especially concerning climatic data (Ranjitkar et al. 2016). However, other variables besides climatic factors are needed because other variables will affect species distribution (Bucklin et al. 2015), such as land cover and anthropogenic factors. Altitude and geographic location are other variables correlating with species presence and climate. The selection of environmental variables as predictors in developing species distribution models must be general so that the model can be used elsewhere. The more factors used, the more specific the model will be (Cauwer et al. 2014). We used seventeen environmental variables consisted of climate and physical environmental data. Climate data were derived from global climate data (worldclim.org) with a 900 m resolution. Climate data consisted of annual mean temperature (BIO1), seasonal temperature (BIO4, standard deviation x100), maximum dry season temperature (BIO5), minimum rainy season temperature (BIO6), annual rainfall (BIO12), rainy season rainfall (BIO13), dry season rainfall (BIO14), seasonal rainfall (BIO15). Physical environmental data consisted of elevation and slope analyzed from DEMNAS data (tanahair.indonesia.go.id/demnas) with a resolution of 10 m. Land cover data was obtained from the interpretation of Sentinel-2 satellite imagery data, with a 10 m resolution. Evaporation data was taken from NOAA satellite data (earthexplorer.usgs.gov) with a 900 m resolution. Soil type on a 50k scale, bulk density, nitrogen, cation exchange capacity, and soil pH were taken from global soil data (soilgrids.org).

The sampling design for population data collection used a single sample plot measuring 10x10 m. A total of 98 plots with a distance between sample plots of 100 m were applied. The sample plots were divided into several subplots, measuring 2x2 m for seedlings, 5x5 m for saplings, and 10x10 m for trees. Sample plots were spread throughout the Karangsari research station area (Figure 1). The population data of *C. calothyrsus* consisted of data on the number and height of individuals. Meanwhile, the fecundity data observed were data on the number of flower stalks and fruits from 100 trees. *C. calothyrsus* is grouped based on the growth phase (Yudaputra 2020): a) seedling

(individual with a height of <2 m); b) Sapling (individual with a height of 2-12 m); c) tree (individual with a height of >12 m). Sapling and tree are adult growth phase, indicated with the presence of flowers and fruits (Yudaputra 2020).

### Data analysis

The suitable habitat of *C. calothyrsus* was predicted using Maxent. Maxent is one of the ecological niche models often used to predict suitable habitat using presence data (Merow et al. 2014; Katz et al. 2018; Srivastava et al. 2019), has good predictive performance (Keith et al. 2014; Peterson et al. 2015), and can provide much more robust results mainly when applied to small sample sizes. Maxent has been successfully applied to model the distribution of invasive species (Srivastava et al. 2019; Yudaputra 2020). The occurrences data of *C. calothyrsus*, which has been recorded, were then resampled using the ArcGIS application. Data resampling aims to ensure the occurrences data of *C. calothyrsus*, which represents the pixel layers of the predictor (environmental variable data), does not indicate spatial autocorrelation so that potential bias in model development can be avoided (Brown and Yoder 2015). A total of 411 *C. calothyrsus* occurrence data were collected through field surveys in 2023 and data from the TNGC 2015 Invasive Plant Mapping and Control Report (BTNGC 2015). Based on the resampling analysis, only 361 *C. Calothyrsus* occurrence data were used in this study, while the other 50 occurrence data indicated spatial autocorrelation at a resolution of 10 m. The differences in occurrence data will not affect the accuracy of the Maxent modeling results used in the study (Elith and Leathwick 2009; Xiong et al. 2019; Fang et al. 2021).

A resample and rescale analysis to match data resolution was carried out using environmental variables at 10 m resolution. Seventeen environmental variables, consisting of climate and physical variable data, were used to predict *C. calothyrsus* distribution. However, the dependence between variables is possibly high, so a collinearity test is needed. Collinearity tests were carried out to 17 environmental variables to avoid collinearity between environmental variables to ensure that each variable is not interdependent. Strong collinearity will result in misinterpretation of the model (Cruz-Cárdenas et al. 2014) and reduce predictive power and interpretability. Environmental variables that have high spatial correlation (Pearson correlation >0.75) were not used (Xiong et al. 2019). Based on the collinearity test, it was found that four environmental variables had a robust relationship ( $p > 75$ ), namely the maximum temperature of the dry season (BIO5), the minimum temperature of the rainy season (BIO6), the rainfall of the dry season (BIO14) and nitrogen. So, only 13 environmental variables were used as predictors to develop *C. calothyrsus* habitat suitability model. These environmental variables were annual average temperature (BIO1), seasonal temperature (BIO4, standard deviation x100), annual rainfall (BIO12), rainy season rainfall (BIO13), seasonal rainfall (BIO15), elevation, slope, land cover, evapotranspiration, soil type, bulk density, cation exchange capacity, and soil pH.

The occurrences data of *C. calothyrsus* and environmental variables data were imported into Maxent to predict the current suitable areas. A total of 75% of the occurrences data of *C. calothyrsus* were used as the training set, and the remaining 25% were used as the random test set; this was done to reduce the potential uncertainty caused by sampling. Five replications were performed to validate the robustness of the model (Feng et al. 2019), with a maximum of 5,000 iterations (Phillips et al. 2017) and 10,000 background numbers set to find the optimal solution, with other parameters kept at default values (Xiong et al. 2019, 2020). The Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC) plot in Maxent was used to evaluate the model's discrimination ability. The AUC criteria were defined as follows: poor (AUC <0.75), good (AUC 0.85-0.95), and excellent (AUC >0.95) (Srivastava et al. 2019). The relative contribution of various bioclimatic predictors to the distribution model was evaluated using the percentage contribution of variables and Jackknife, which can identify variables that have the most significant impact on the overall model (Xiong et al. 2020). Habitat suitability maps were constructed using the ten percentile training occurrences Cloglog threshold (P10). This threshold removes records with <10% habitat suitability during model training based on the assumption that remote locations do not represent the habitat in general (Crawshaw et al. 2022). Categorical classification in the ArcMap software package created habitat suitability classifications. Habitat suitability is classified into two categories based on the P10 value, namely unsuitable habitat (<P10) and suitable habitat (>P10) (Crawshaw et al. 2022).

Population dynamics were analyzed using the Leslie matrix (Caswell 2001). The Leslie matrix model effectively estimates population growth based on age structure (Donovan and Welden 2002). The population of *C. calothyrsus* was grouped into three levels of structure based on its growth form: seedlings, saplings, and trees. So, size is a good predictor of birth rates compared to age. The size or stage-structured matrix model is suitable for use (Lefkovich 1965; Caswell 2001; Donovan and Welden 2002). The Leslie matrix helps analyze population classes, namely for analyzing the probability of seedlings growing into saplings (stage G1) and the probability of saplings growing into individual trees (stage G2). The characteristics of the population dynamics of *C. calothyrsus* were obtained by observing the values and eigenvectors of the matrix.

Analysis of the spatial distribution of *C. calothyrsus* populations at the landscape level was carried out using RANGESHIFTER software version 2.0. (Bocedi et al. 2021). The simulation of the dynamics of the distribution of *C. calothyrsus* populations applied for 50 years. In the simulation, the minimum age of adult *C. calothyrsus* was set at one year, survival probability of 0.8, density independence of 0.1, and death probability of 0.2. When finding unsuitable cells, individuals were set to select suitable cells randomly. The average distance used for distribution was 50 m, and the simulation was run with two replications. The density of individuals was inputted according to calculations based on cell resolution, and the proportion of individuals per growth structure was 0.7 (S1): 0.3 (S2). In addition to population dynamics data, RANGESHIFTER software version 2.0. requires spatial data in the form of landscape characteristics. Landscape characteristics are compiled by conducting spatial analysis of land cover map prepared using sentinel-2 path/row 121/65 image data recorded on 10 August 2019. Supervised classification with the Maximum Likelihood Classification method was applied to interpret land cover. The results of the interpretation accuracy test showed a Kappa value of 9.18 and an overall accuracy of 93.42 (Figure 1).

## RESULTS AND DISCUSSION

### Population of *Calliandra calothyrsus* at the sampling site in Gunung Ciremai National Park

The total population of *C. calothyrsus* at the sampling site in GCNP was recorded at 1,581 individuals with a density of 21,529.08 indv/ha. The proportion at each growth phase was seedlings 47.06%, saplings 35.04%, and trees 17.90%. The height of *C. calothyrsus* individuals is related to the growth phase. The seedlings are defined as individuals that have not produced flowers and fruits with a height of <2 m. The saplings and trees are those that have been able to flower and bear fruit and have a height of >2 m which composed 52.94% of total population (Table 1). The fecundity value was analyzed based on the percentage of the number of flowers that later became fruit (Hewitt et al. 2014). The flowering and fruiting period of *C. calothyrsus* in GCNP lasts 3-4 months, from June to September (Ismail et al. 2022). The fecundity of *C. calothyrsus* in the sapling growth phase is 0.94, and in the tree growth phase is 0.83.

**Table 1.** Population and density of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia, at each growth phase and reproductivity

Growth phase	Populations	Density (ind/ha)	Non-reproductive individual (height <2 m)	Reproductive individual (height >2 m)
Seedling	744	18,979.59	744	837
Sapling	554	2,261.22		
Tree	283	288.27		

*C. calothyrsus* has a different growth stage structure related to its reproduction process. These stages consist of individuals who can reproduce and those who are unable to reproduce. Individuals unable to reproduce are grouped into the seedling growth phase, and those who can reproduce are grouped into the sapling and tree growth phases. The life cycle of *C. calothyrsus* is presented in Figure 2.

Based on the population of *C. calothyrsus* at each growth phase, it can be determined that  $G_{2,1}$  (the ability to survive and develop seedlings to the sapling growth stage) is 0.74.  $G_{2,2}$  (the ability to survive and develop saplings to the tree growth stage) is 0.51.  $P_{2,2}$  (the ability to survive the sapling growth stage and remain at the sapling growth stage) is 0.26. Moreover,  $P_{2,3}$  (namely the ability to survive the tree growth stage and remain at the sapling growth stage) is 0.49. The fecundity of at sapling stage ( $F_{1,2}$ ) is 0.94, and the fecundity at tree stage ( $F_{1,3}$ ) is 0.83. The population matrix model of *C. calothyrsus* can be written as follows:

$$L = \begin{bmatrix} 0 & 0.94 & 0.83 \\ 0.74 & 0.26 & 0 \\ 0 & 0.51 & 0.49 \end{bmatrix}$$

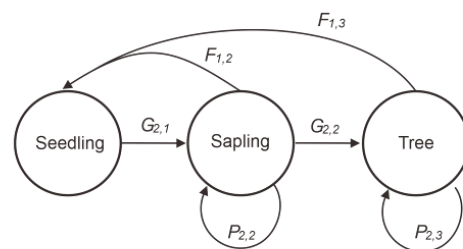
The eigenvalue of the population matrix of *C. calothyrsus* is  $\lambda$ : 1.20 with eigenvectors  $x_1$ : 1;  $x_2$ : 0.78; and  $x_3$ : 0.56. The highest matrix elasticity is the transition from the seedling growth phase to the sapling phase, with a value of 0.34.

### Predicted suitable habitat of *Calliandra calothyrsus* in Gunung Ciremai National Park

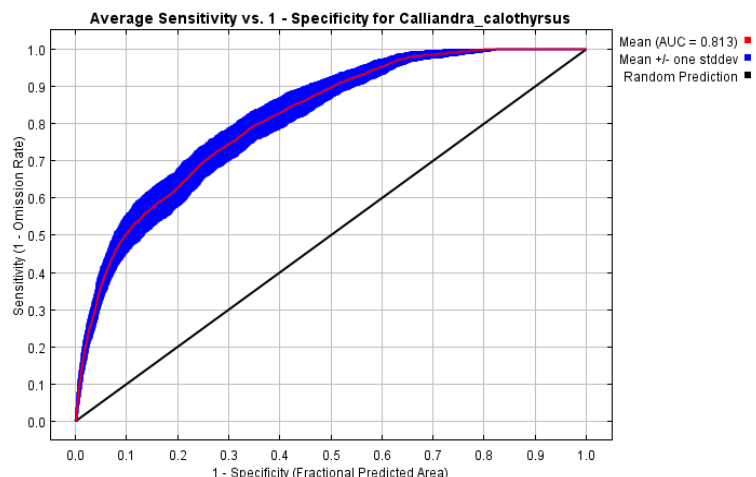
The accuracy of habitat suitability model of *C. calothyrsus* was measured using the AUC value. The AUC value produced by the Maxent simulation was 0.813 with a standard deviation of 0.20 (Figure 3). This value indicates that the model performance is good (Srivastava et al. 2019) although it differed with other study using similar species (Yudaputra 2020) which is due to the use of different resolutions. The data resolution used in this study was 10 m

while Yudaputra (2020) used 900 m. Differences in data resolution can cause differences in the accuracy of the resulting model (Alsamadisi et al. 2020). In addition, the number and type of predictors can also cause predictive power and interpretability. Five climate data variables and five environmental physical data variables were used by Yudaputra (2020), namely BIO1, BIO4, BIO12, BIO13, and BIO15 for climate data variables and elevation, land cover, evapotranspiration, soil type, and soil pH for environmental physical data variables. This study used five climate data variables and eight environmental and physical variables, including edaphic data variables. The different variables from Yudaputra (2020) are slope, bulk density, and cation exchange capacity. The rationale on the use of climate variables as model predictors because changes in the composition of plant communities are influenced by climate factors (Li et al. 2020). Edaphic variables such as soil type influence the spread of invasive plants significantly.

Based on the habitat suitability model of *C. calothyrsus*, it was identified that 8,199.395 ha (55.25%) of the GCNP is not suitable for *C. calothyrsus*, while the remaining 6,641.905 ha (44.75%) is suitable (Figure 4).

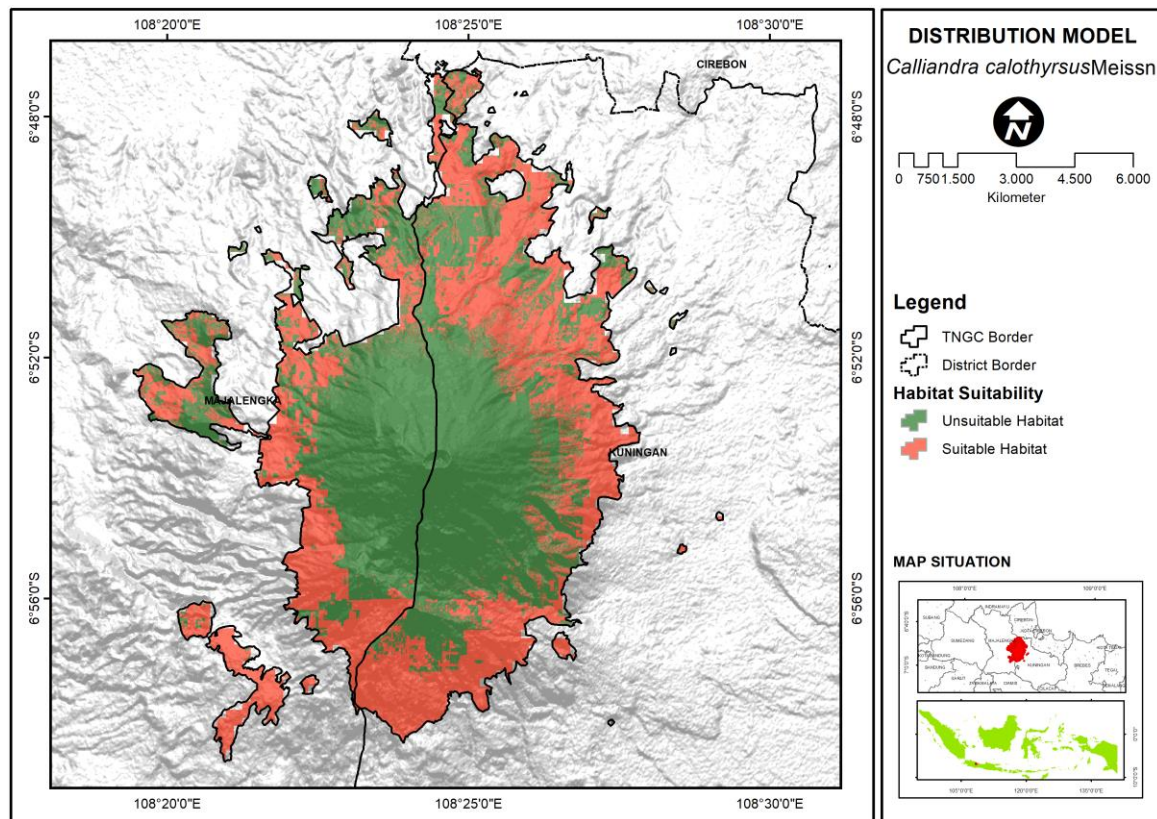


**Figure 2.** The life cycle of *Calliandra calothyrsus* at three growth stages



**Figure 3.** The ROC and AUC values resulted from the Maxent analysis to model suitable habitat of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia





**Figure 4.** Map of predicted suitable habitat of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java, Indonesia, modeled using Maxent

Three model predictors that had a dominant contribution to the habitat suitability model of *C. calothyrsus* were identified, namely land cover (47.9%), rainfall (20.7%), and temperature (16.1%) (Table 2). Annual rainfall (BIO12) and seasonal temperature (BIO4) contributed 20.7% and 16.1% but did not indicate the level of specific habitat suitability for *C. calothyrsus*. Meanwhile, the land cover provided the most helpful information on the distribution of *C. calothyrsus* in GCNP (Figure 5). Land cover type is a discriminant predictor compared to the similar study by Yudaputra (2020), which concluded that the predictors for suitable habitat of *C. calothyrsus* are elevation, evapotranspiration, rainfall, and temperature. Meanwhile, the land cover variable only has a relative importance value of 10% for the model.

Rainfall and temperature are primary factors that influence the distribution of plant communities (Li et al. 2020). *C. calothyrsus* can grow in humid and semi-humid habitats in primary, secondary, or disturbed lowlands to sub-montane, seasonally dry to wet subtropical forests, oak forests, pine forests, and shrubs. The best development of *C. calothyrsus* occurs at medium altitudes below 1,300 masl. In Java, the species is planted up to an altitude of 1,500 masl but grows best between 250-800 masl in areas with an annual rainfall of 2000-4000 mm and 3-6 months of dry season. Daily temperatures between 22-28°C, maximum monthly environmental temperature growth tolerance between 24 and 30°C, and minimum between 18

and 22°C (Macqueen 1996; Orwa et al. 2009). *C. calothyrsus* shows a high level of habitat suitability in shrub but a low level in plantation and forest. *C. calothyrsus* grows well in full light conditions, is intolerant of full shade conditions, and is quite tolerant of moderate shade conditions.

**Table 2.** The contribution of predictors to habitat suitability model of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia

Predictors	PC (%)	PI (%)
Annual Mean Temperature (BIO1)	0.2	0.9
Seasonal Temperature (BIO4, standard deviation x100)	<b>16.1</b>	17.6
Annual Rainfall (BIO12)	<b>20.7</b>	12.3
Wet Season Rainfall (BIO13)	3.9	6.4
Seasonal Rainfall (BIO15)	1.7	5.5
Elevation	0.3	6.3
Slope	2.2	1.6
Land Cover	<b>47.9</b>	33.7
Evapotranspiration	0.6	0.8
Soil Type	2.5	3.1
pH	0.1	0.2
Cation Exchange Capacity	3.7	11.3
Bulk Density	0.1	0.3

Note: PC: Percent Contribution; PI: Permutation Important; Bold numbers indicate the largest PC

### Population dynamics and dispersal of *Calliandra calothyrsus* in Gunung Ciremai National Park

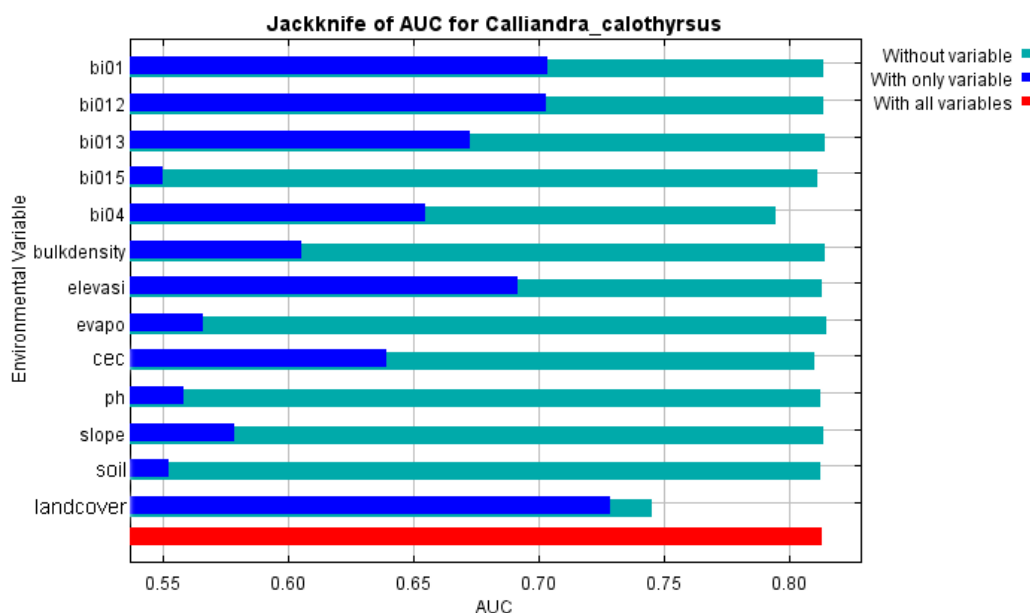
Combining population growth data with spatial data analysis can provide an understanding of population distribution at the landscape level (Yudaputra and Sudarmono 2019; Yudaputra 2020). The population structure of *C. calothyrsus* in GCNP is included at the stage of developing population, with growth being slow from year 0 to year 10. A significant increase occurred from year 10 to year 50 (Figure 6).

The distribution of *C. calothyrsus* is in line with population growth; the average occupancy suitability during the simulation was 26.93%, with a standard deviation of 0.00029 (Table 3). *C. calothyrsus* dynamically continues to spread and occupy the research area. The dominance of the population size of *C. calothyrsus* indicates a low population size. Population size can be

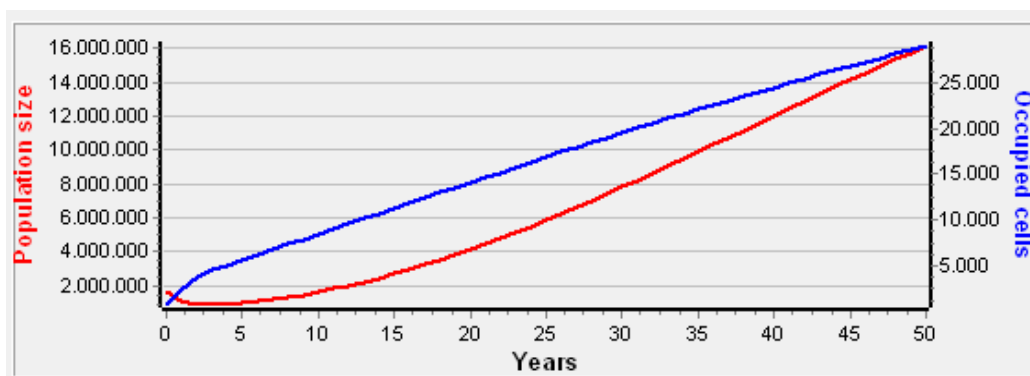
interpreted as the *C. calothyrsus* population dominated by the seedling growth phase, higher than the sapling and tree growth phase (Figure 7).

**Table 3.** Mean and standard deviation of occupancy suitability of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia, throughout 50 years of simulation

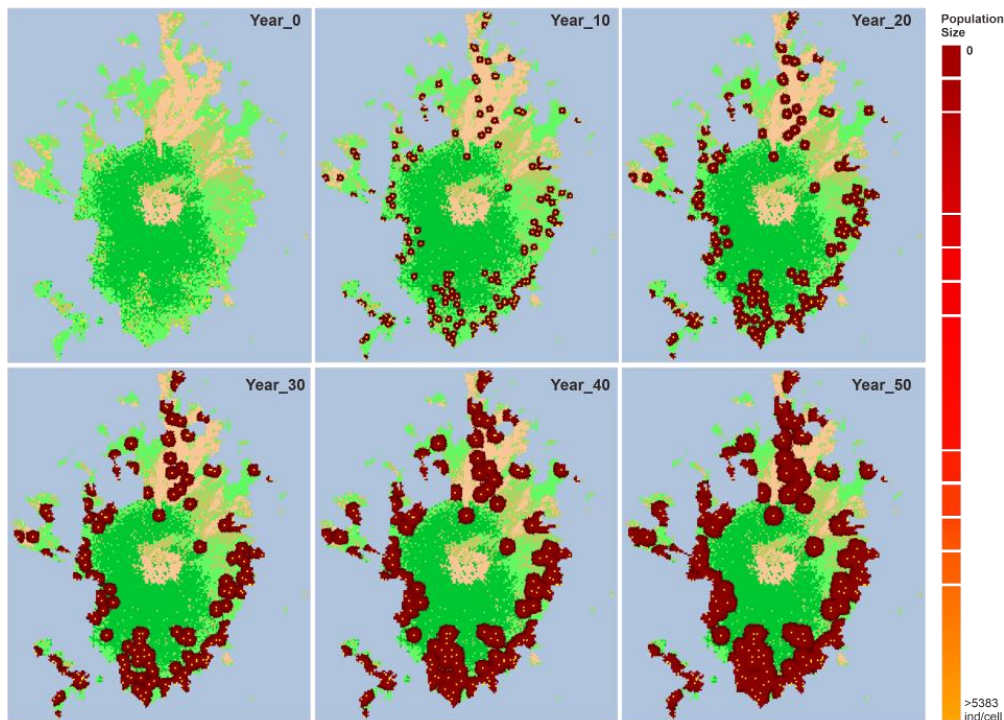
Year	Mean_OccupSuit	Std_error
0	0.010625	0.000000
10	0.140509	0.000042
20	0.236214	0.000271
30	0.328598	0.000042
40	0.411542	0.000382
50	0.488307	0.001003



**Figure 5.** Jackknife test of model distribution of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia



**Figure 6.** Population dynamic of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia, throughout 50 years of simulation



**Figure 7.** The population dispersal of *Calliandra calothyrsus* in Gunung Ciremai National Park, West Java Province, Indonesia, throughout 50 years of simulation

The most influential population parameter on plant growth is size or growth stage (Donovan and Welden 2002). Individuals with different sizes or stages have very different potentials to influence future population size (Bierzychudek 2014). The use of size classes or growth stages provides many possibilities in plant growth, namely the movement of size classes to larger classes, the movement of size classes to smaller classes, remaining in the same size class, or dying (Bierzychudek 2014). To manage this complexity and provide a sense of order, structured matrix models are used to model plant population dynamics (Bierzychudek 2014). The Leslie matrix (Lefkovich 1965; Caswell 2001) is a matrix model that has been widely used (Barraquanda and Gimenez 2019; Takada and Kawai 2020; Vries et al. 2020; Yudaputra 2020; Guo et al. 2021).

The population structure of *C. calothyrsus* in GCNP based on its growth class is divided into three growth phase classes: seedlings, saplings, and trees. The seedling growth phase is the most dominant structural class. This structural class is found in almost all observation plots. The population dynamics of *C. calothyrsus* increased significantly in ten years of simulation. The increase is possible because fecundity is relatively high in the sapling growth phase (0.94) and trees (0.83). In the long term, *C. calothyrsus* will be able to produce seeds in large quantities (Yudaputra 2020). The fecundity and plant size are also correlated with the level of invasiveness (Jelbert et al. 2015). Referring to the results of the elasticity analysis of the transition matrix, the vital thing related to the increase in the growth rate of *C. calothyrsus* is the growth from the

seedling stage to the tree with a proportion of 0.34. Given that the fecundity value at this stage is quite significant, this condition will also impact considerable population growth.

The dynamics of population dispersal of *C. calothyrsus* is built based on a stochastic distribution model by considering various random possibilities, both demographic stochastic and environmental stochastic. In the *C. calothyrsus* distribution, demographic stochastic is based on fecundity, survival, and mortality factors. Meanwhile, the environmental stochastic is set constantly at 0.1. In the early stages of distribution, the population structure of *C. calothyrsus* occurs with low density. However, later in disturbed areas, this species will invade areas with high vegetation density (Macqueen 1992; Hendrati et al. 2014). The research location's land cover consists of forest land, pine forest, shrubs, and bare land. Invasive plants invade the forest cover class with low vegetation density and separate small patches (Gaol and Mudita 2020; Dann et al. 2024). So, the three types of land cover also have the potential to be invaded by *C. calothyrsus*.

In conclusion, *C. calothyrsus* GCNP shows an increasing population structure where the seedlings grow into poles. Meanwhile, bareland and shrubland significantly influence *C. calothyrsus*'s distribution. Controlling the rate of growth from the seedlings to the poles and restoring the ecosystem shrubs and open land to control the distribution of *C. calothyrsus* are two management strategies that can be used to suppress the population growth of this species.



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